

Sharpened cortical tuning and enhanced cortico-cortical communication contribute to the long-term neural mechanisms of visual motion perceptual learning



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investigate what longer-lasting neural changes may be associated with VPL.

In our current investigation, we studied visual motion perceptual learning, with two specific aims: whether the neural modifications occurred at low- or high-level, and what neural modifications may be longer-lasting. Human subjects were trained in a motion direction discrimination task. Their behavioral performance and BOLD signals were measured before, immediately after, and two weeks after training. We examined not only how learning affected the local representation of the trained motion direction within individual visual cortical areas and IPS, a motion decision-making area and homologue of monkey LIP (lateral intraparietal area) (Kayser et al., 2010), but also how learning changed the effective connectivities between the visual areas and IPS. Law and Gold (2008, 2009) modeled the learning process as a high-level decision unit refining its connectivities to sensory neurons tuned to a specific motion direction through response reweighting (Poggio et al., 1992; Doshier and Lu, 1998; Bejjanki et al., 2011). However, there is no empirical evidence yet directly supporting this hypothesis.

Here, we report that, parallel to the long-lasting motion discrimination improvement, the neural selectivity in V3A and the effective connectivity from V3A to IPS for the trained direction exhibited a persistent increase after training, as revealed by both decoding and encoding analyses and dynamic causal modeling (DCM). We found that the behavioral learning could be well explained by a linear combination of improvements from these two sources. These findings make headways towards resolving previous controversies and demonstrate that perceptual learning should be attributed to

averaged, and then plotted as a function of training day. The learning curves were fitted with a power function (Jeter et al., 2009).

During the three test phases, psychophysical and fMRI tests were performed at four motion directions, which were 0°, 30°, 60°, and 90° deviated from the trained direction all either clockwise or counter-clockwise (hereafter referred to as 0°, 30°, 60°, and 90°). We first measured motion direction discrimination thresholds at these four directions. Ten QUEST staircases (same as above) were completed for each direction. The four directions were counterbalanced for individual subjects. Discrimination thresholds from the 10 staircases for each direction were averaged as a measure of subjects' discrimination performance. Subjects' performance improvement at a direction was calculated as $(\text{pre-training threshold} - \text{post-training threshold}) / \text{pre-training threshold} \times 100\%$.

After acquiring psychophysical discrimination thresholds, we mea-

block, resulting in 32 beta value patterns per test for each stimulus condition and ROI. For the decoding analysis, we trained linear support vector machine (SVM) classifiers (www.csie.ntu.edu.tw/~cjlin/libsvm) using these patterns per ROI and calculated mean decoding accuracies following a leave-one-run-out cross validation procedure. That is, we trained one-against-one binary classifiers (e.g., 30° vs. 90°) on 30 training patterns and tested their accuracy on the remaining two patterns per stimulus condition and ROI using a 16-fold cross-validation procedure. These binary classifiers were used to construct a four-way classifier for decoding the four motion directions (Kamitani and Tong, 2005; Preston et al., 2008; Serences et al., 2009; Zhang et al., 2010a). The chance performance for the four-way classifier was 0.25. Similar to the LMI for BOLD amplitudes, we defined the LMI for decoding accuracy as $[Acc(\text{trained direction post-training}) - Acc(\text{trained direction pre-training})] - [Acc(\text{untrained directions post-training}) - Acc(\text{untrained directions pre-training})]$, where Acc stands for decoding accuracy. The decoding accuracy for the untrained directions was the average accuracy for the 30°, 60°, and 90° directions.

Multivariate analysis – forward model

The decoding analysis is a sensitive tool to detect changes in spatial activation pattern, as reflected by changes in decoding accuracy. However, this analysis by itself cannot tell how or why a change occurred. For example, improved decoding accuracy in an ROI could reflect improved stimulus selectivity, or reduced noise level, or some other factors. The forward modeling analysis (Brouwer and Heeger, 2009, 2011; Saproo and Serences, 2014) provides a way to probe the stimulus selectivity issue. It has been suggested that perceptual learning could improve the neural selectivity for trained stimuli (Schoups et al., 2001; Zhang et al., 2010a). In practice, the decoding analysis and the forward modeling analysis can be used in a complementary manner. The decoding analysis usually serves as an initial tool for an exploratory purpose to identify cortical areas carrying some information about an experimental manipulation (e.g., learning). Then a forward model can be developed to characterize the underlying neural mechanisms in these areas (Serences and Saproo, 2012).

For an ROI showing a decoding accuracy change, we used the forward model described by Brouwer and Heeger (2009) to estimate the magnitude of responses in direction-selective neuronal populations in the ROI before and after training. The model decomposed voxel responses into a set of hypothetical direction-selective channel responses (Saproo and Serences, 2014), assuming that BOLD responses from voxels in the ROI reflect an approximately linear mixture of responses from many subpopulations of neurons with different degrees of selectivity to different directions of motion (Boynton et al., 1996; Heeger et al., 2000; Logothetis and Wandell, 2004; Kahnt et al., 2011).

The BOLD response of each voxel for each of the four motion directions (i.e., the trained and untrained directions) was modeled as a linear sum of weighted responses of 12 different direction-selective channels, with the direction selectivity of the channels linearly spaced between 0° and 360° (0°, 30°, 60°, ..., 330°). The tuning profile of each channel was modeled using a sinusoidal function raised to the fourth power (Saproo and Serences, 2014).

The computation consisted of two stages. The first stage was to estimate the weights on the 12 hypothetical channels separately for each voxel. With these weights, the second stage was to compute the channel outputs associated with the spatially distributed pattern of BOLD signal across voxels evoked by the motion directions. In other words, this stage allowed us to transform the voxel responses to the channel responses, each tuned to a different direction.

Recall that, there were 32 spatial patterns of voxel response (i.e., beta value) per test for each motion direction and ROI. These 32 patterns were divided into a training set (30 patterns) and a test set (2 patterns). The training set was used to estimate the channel weights

in the first stage and the test set was used to compute the channel responses in the second stage. In the first stage, the weight of each channel in response to each of the four directions was estimated using a standard GLM (Eq. 1). Let k be the number of channels, m the number of voxels, and n the number of repeated measurements (i.e., 4 directions \times 30 patterns in the training set). The matrix of voxel responses in the training set ($B_1, m \times n$) was related to the matrix of hypothetical channel outputs ($C_1, k \times n$) by a weight matrix ($W, m \times k$).

$$B_1 = WC_1 \quad (1)$$

The ordinary least-squares estimate of W is computed as follows:

$$\hat{W} = B_1 C_1^T (C_1 C_1^T)^{-1}. \quad (2)$$

In the second stage, the pattern of voxel response in the test set B_2 was used to compute the estimated channel responses C_2 using the previously computed weights W .

$$C_2 = (\hat{W}^T \hat{W})^{-1} \hat{W}^T B_2 \quad (3)$$

The training/testing procedure was repeated for all combinations of the 32 patterns. Finally, the channel response profile computed each time was circularly shifted such that the motion direction that evoked the response profile was set to 0° offset in the abscissa of Fig. 6. The responses were further collapsed across channels with the same magnitude of channel offset, but opposite signs (i.e., positive and negative).

Dynamic causal modeling (DCM)

The DCM analysis was performed to examine whether there was any connectivity change between sensory areas (e.g., V3A and MT+) and decision-making areas (e.g., IPS) after training. Effective connectivities between V3A and IPS and between MT+ and IPS were analyzed with the DCM (Friston et al., 2003; Friston, 2006) in SPM10. For each of these areas in both hemispheres, voxels within a 5-mm-radius sphere centered on the most responsive voxel in the localizer run were extracted, and their time series were used for the DCM analysis. The estimated DCM parameters were later averaged across two hemispheres using the Bayesian model averaging method (Friston, 2006). The mean MNI coordinates of these voxels and the SEs across subjects in V3A, MT+, and IPS were $[28.5 \pm 1.4, -86.9 \pm 1.7, 10.4 \pm 1.6]$, $[44.2 \pm 0.9, -65.6 \pm 1.6, 7.0 \pm 1.5]$, and $[25.4 \pm 1.7, -58.6 \pm 2.3, 52.1 \pm 1.3]$ for the right hemisphere; and $[-27.0 \pm 0.9, -90.3 \pm 2.2, 13.9 \pm 2.5]$, $[-50.0 \pm 1.1, -70.7 \pm 1.4, 7.9 \pm 1.7]$, and $[-27.0 \pm 2.0, -57.8 \pm 2.9, 52.4 \pm 1.7]$ for the left hemisphere, respectively.

DCMs have three sets of parameters: extrinsic inputs into one or more regions, intrinsic connectivities among the modeled regions, and bilinear parameters encoding the modulation of the specified intrinsic connections by experimental manipulations. The third set of parameters are used to quantify modulatory effects, which reflect increases or decreases in connectivity between two regions given some experimental manipulation, compared with the intrinsic connections between the same regions that capture connectivity in the absence of experimental manipulation. fMRI data were modeled with a GLM procedure, including regressors for the trained and untrained directions, as well as a condition comprising all the directions (i.e., the extrinsic input to V3A and MT+). Bidirectional intrinsic connections were hypothesized to exist between V3A and IPS and between MT+ and IPS, and these connections were modulated by our experimental manipulations (i.e., the modulatory input) (Fig. 7A). The modulatory input could be either the trained direction or the untrained directions. We examined three models for modeling the modulatory effect by the trained or the untrained directions, including feedforward, feedback, and recurrent

models. We fitted each of these three models for each subject. Using a hierarchical Bayesian approach (Friston, 2006), we compared the three models by computing the exceedance probability of each model, i.e., the probability to which a given model is more likely than the other two models to have generated data from a randomly selected subject. In the best model, we examined changes in the modulatory effects by the trained and untrained directions at Post1 and Post2, relative to Pre. In the psychophysical and fMRI data analyses, Bonferroni correction was applied with t-tests and ANOVAs involving multiple comparisons.

Results

Psychophysical results

Subjects underwent eight daily training sessions (1000 trials per session) to discriminate motion directions around a pre-specified, but randomly selected direction (hereafter the direction is referred to as 0°). In a trial, two random-dot kinematograms (RDKs) with slightly different directions were presented sequentially. Subjects were asked to make a two-alternative forced-choice (2-AFC) judgment of the direction of the second RDK relative to the first one (clockwise or counter-clockwise) (Fig. 1A). The QUEST staircase was used to control the direction difference between the two RDKs adaptively to estimate subjects' motion direction discrimination thresholds at 75% correct. Throughout the training, subjects' discrimination thresholds gradually decreased and saturated after day 6 (Fig. 2A). The thresholds on days 7 and 8 were not significantly different from that on day 6 (both $t(16) < 1.39$, $p > 0.05$). Note that, in our psychophysical and fMRI data analyses, Bonferroni correction was applied with t-tests and ANOVAs involving multiple comparisons.

Psychophysical and fMRI tests were performed on the days before (Pre), immediately after (Post1), and two weeks after training (Post2) (Fig. 1B). We first measured motion direction discrimination thresholds at the trained direction, as well as at the untrained directions

that were 30°, 60°, and 90° away from the trained direction. The discrimination thresholds were submitted to a repeated-measures ANOVA with test (Pre, Post1, and Post2) and direction (0°, 30°, 60°, and 90°) as within-subject factors. We found a significant main effect of test ($F(2,32) = 16.73$, $p < 0.01$) and a significant interaction between test and direction ($F(6,96) = 16.78$, $p < 0.01$) (Fig. 2B). To compare the learning effects at the trained and untrained directions, we calculated the percent improvements in discrimination performance after training. The improvement for the trained direction at Post1 and Post2 were 41% and 33%, respectively, which were significantly higher than those for the untrained directions (<15%) (all $t(16) > 3.4$, $p < 0.01$) (Fig. 2C). These results demonstrated that training led to a significant learning effect, with the trained direction showing significantly greater improvement than the untrained directions.

persisted for at least two weeks after training, if any training-induced neural change is considered to constitute the neural mechanisms of the learning, the change should manifest at both Post1 and Post2. Note that subjects showed a similar behavioral learning effect for the three untrained directions, suggesting that training-induced neural changes (if there were any) associated with these three directions might be similar. For all the fMRI data analyses (including the univariate analysis, the multivariate analyses, and the DCM analysis), we not only compared the data between the trained direction and each of the untrained directions, but also compared the data for the trained direction with the averaged data for the untrained directions. Since the results of the comparisons were very similar, for the sake of simplicity, we chose to present the comparison between the trained direction and the average of the untrained directions.

With the univariate analysis, we examined whether training could change the mean BOLD amplitude for the trained direction when compared with the untrained directions. For each ROI, BOLD amplitudes (i.e., beta values) for the trained and untrained directions were estimated with a general linear model (GLM). Beta values were submitted to a repeated-measures ANOVA with test (Pre, Post1, and Post2) and direction (trained and untrained) as within-subject factors. A significant interaction between test and direction was found only in V3A ($F(2,32) = 6.57, p < 0.05$), suggesting that training had different effects on the mean BOLD amplitudes evoked by the trained and untrained directions in this area (Fig. 3A).

To isolate the BOLD amplitude change that was specific to the trained direction and to distinguish it from general practice effects or common sources of variance, we defined the learning modulation index (LMI) for BOLD amplitude as $[Amp(\text{trained direction post-training}) - Amp(\text{trained direction pre-training})] - [Amp(\text{untrained directions post-training}) - Amp$

$(\text{untrained directions pre-training})]$. The LMI quantified the amplitude difference for the trained direction before and after training while subtracting out the difference for the untrained directions. An index significantly above/below zero indicates that training increased/decreased the BOLD signal to the trained direction. We calculated the LMI for BOLD amplitude in V3A because only this area showed a significant interaction effect in the ANOVA above. At Post1, the index, though very small, was significantly lower than zero ($t(16) = 4.35, p < 0.01$). However, relative to Post1, the magnitude of the index decreased at Post2 ($t(16) = 2.35, p < 0.05$), and was not significantly different from zero (Fig. 3B). These results demonstrated that training decreased the cortical response in V3A to the trained direction immediately after training, but the decrease vanished two weeks later even though the improved behavioral performance was largely maintained. This finding suggests that changes in mean BOLD amplitude might not play a critical role in the long-term neural mechanisms of the motion perceptual learning.

Decoding analysis of fMRI data

Since the univariate analysis failed to detect long-term neural changes associated with the persistent behavioral learning effect, we then performed the more sensitive multivariate analysis to examine whether perceptual learning could modify the spatially distributed activation pattern evoked by the trained direction across all voxels within an ROI. More specifi

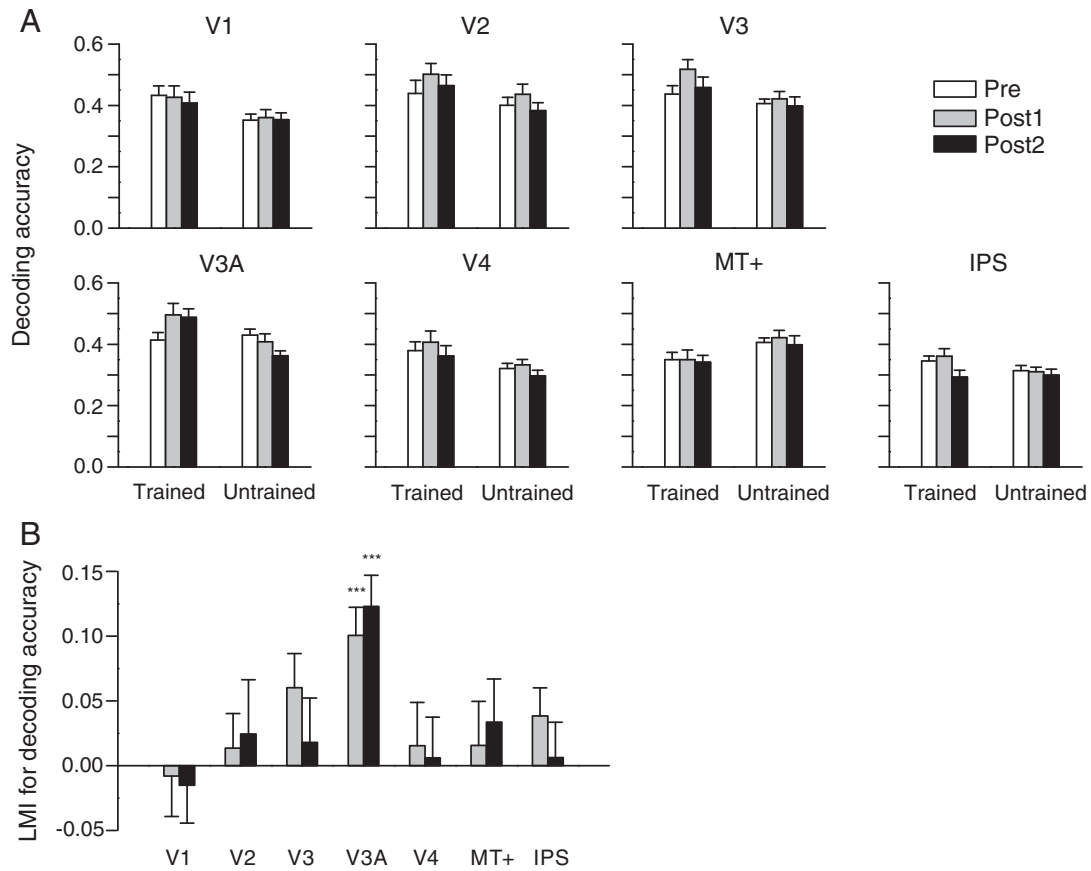


Fig. 4. Results of the multivariate pattern analysis of fMRI data. (A) Decoding accuracies for the trained and untrained directions. (B) LMIs for decoding accuracy. Asterisks indicate the index significantly above zero (***) $p < 0.001$). Error bars denote 1 SEM across subjects.

and calculated the decoding accuracy following a leave-one-run-out cross validation procedure.

Decoding accuracies were submitted to a repeated-measures ANOVA with test (Pre, Post1, and Post2) and direction (trained and

untrained) as within-subject factors. A significant interaction between test and direction was found in V3A ($F(2,32) = 19.07$, $p < 0.001$), suggesting that training may have different effects on the decoding accuracies for the trained and untrained directions in this area

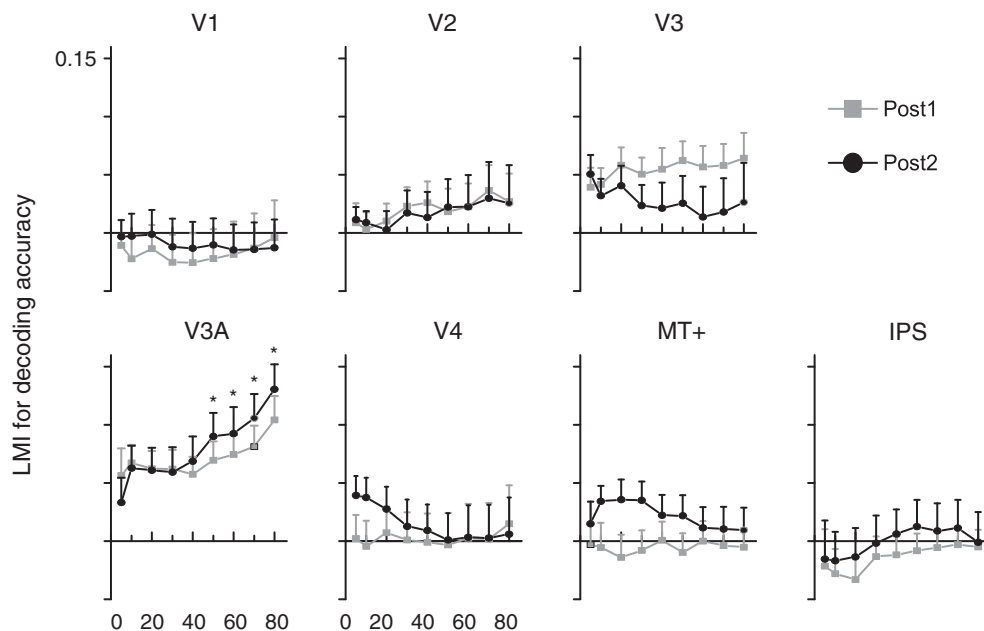


Fig. 5. LMIs for decoding accuracy as a function of voxel number. Asterisks indicate the indexes that are significantly above zero (*) $p < 0.05$). Error bars denote 1 SEM across subjects.

(Fig. 4A). Similar to the LMI for BOLD amplitude, we defined the LMI for decoding accuracy as $[Acc(\text{trained direction post-training}) - Acc(\text{trained direction pre-training})] - [Acc(\text{untrained directions post-training}) - Acc(\text{untrained directions pre-training})]$. We found that V3A exhibited a significantly positive LMI for decoding accuracy at both Post1 and Post2 (both $t(16) > 4.64$, $p < 0.001$) (Fig. 4B), demonstrating that the improved decoding accuracy in V3A persisted over the entire time course of the measurement.

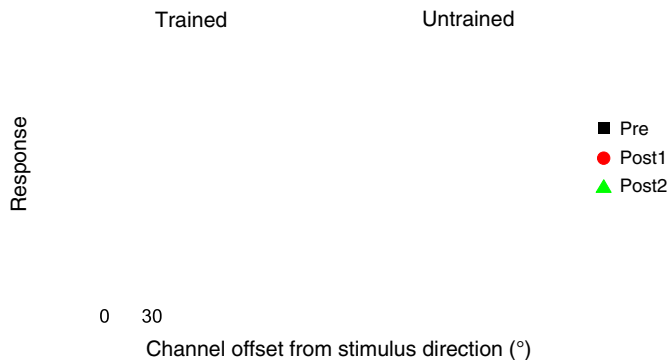
We further examined if this finding depended on the number of selected voxels. For each ROI, we randomly sampled selected 5–80 responsive voxels and performed the decoding analysis. When at least 50 voxels were selected, the LMI for decoding accuracy in V3A was significantly above zero at Post1 and Post2 (all $t(16) > 4.05$, $p < 0.05$) (Fig. 5). Other ROIs did not show a significant positive index within this voxel number range. This result demonstrated that the V3A finding was robust across the selected voxel numbers.

Recall that, in the blocks containing the trained direction, the stimuli were slightly different across Pre, Post1, and Post2. In a trial, the RDKs of 0° and $\pm \Delta\theta$ were presented. $\Delta\theta$ was the discrimination threshold measured in the preceding psychophysical test. Although the 0° RDK was always presented in the three tests, $\Delta\theta$ decreased after training. It is possible therefore that the observed fMRI effects were due to the stimulus difference. To rule out this explanation, at Post1 and Post2, we also measured BOLD signals responding to the same trained direction blocks as those at Pre. We found that, for all the ROIs, using $\Delta\theta$ acquired at Pre had little effect on the beta value (all $t(16) < 2.08$, $p > 0.05$) and the decoding accuracy (all $t(16) < 1.96$, $p > 0.05$) for the trained direction. Furthermore, with $\Delta\theta$ for the trained direction acquired at Pre, the LMI for decoding accuracy in V3A (but not other ROIs) was significantly above zero at Post1 and Post2 (both $t(16) > 3.53$, $p < 0.05$).

Forward modeling analysis of fMRI data

The decoding analysis revealed an increase in decoding accuracy for the trained direction in V3A, suggesting that the neural representation of the trained direction became more separated from those of the untrained directions after training. However, why the change occurred remained unclear. One possibility is that perceptual learning increased the neural selectivity for the trained direction in V3A. To evaluate this possibility, we used a forward model to estimate the magnitude of responses in direction-selective neuronal populations in V3A before and after training. The model decomposed voxel responses into a set of hypothetical direction-selective channel responses.

Fig. 6 shows the direction-selective channel responses for the trained and untrained directions at Pre, Post1, and Post2. For the trained direction, the channel response profile became steeper after training. Repeated-measures ANOVAs revealed significant interactions between



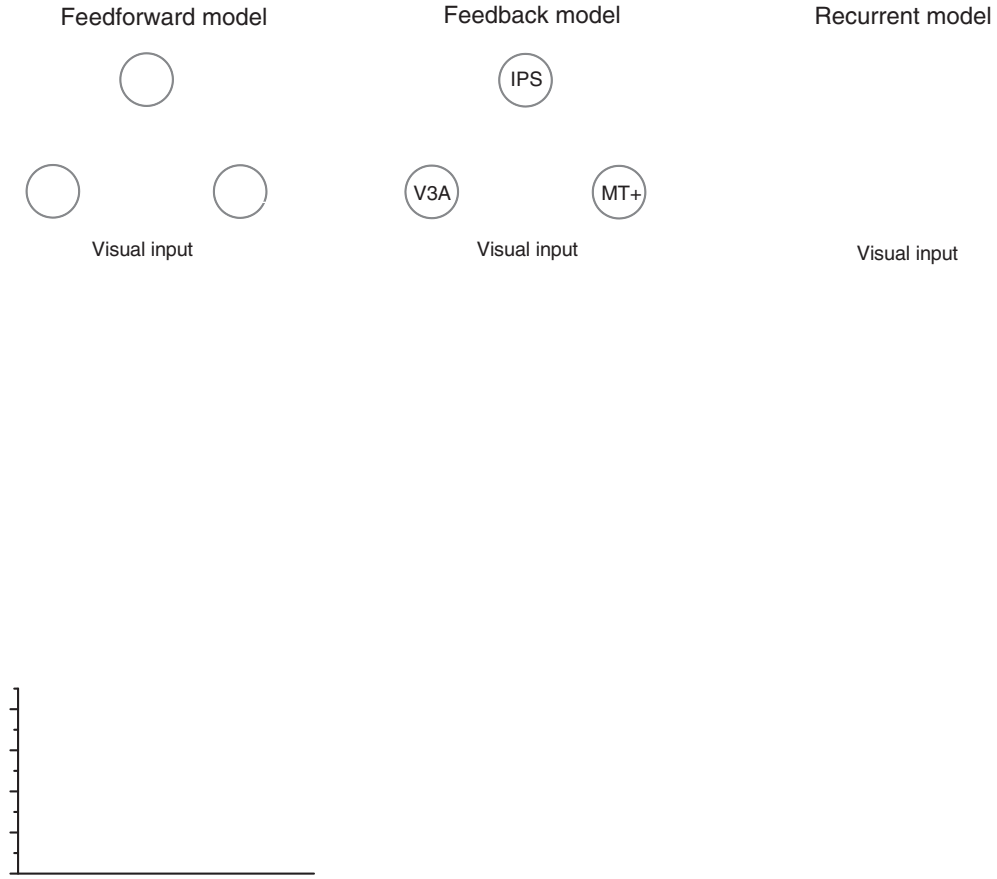
test and channel offset (Pre vs. Post1: $F(4,64) = 9.26$, $p < 0.001$; Pre vs. Post2: $F(4,64) = 5.58$, $p < 0.001$). Relative to Pre, training increased the responses of direction-selective channels tuned to the trained direction (0° offset: $t(16) = 3.40$, $p < 0.001$) and decreased the responses of channels tuned away from the trained direction (60° offset: $t(16) = 2.90$, $p = 0.01$; 90° offset: $t(16) = 2.70$, $p < 0.05$) at Post1. This modulation effect was well preserved at Post2 (0° offset: $t(16) = 2.98$, $p < 0.001$; 60° offset: $t(16) = 2.41$, $p < 0.05$). For the untrained directions, the channel response profile showed little change after training (Pre vs. Post1: $F(4,64) = 0.205$, $p > 0.05$; Pre vs. Post2: $F(4,64) = 0.225$, $p > 0.05$). These results suggest that the persistent behavioral learning effect could be (partially) attributed to the long-term improved neural selectivity for the trained direction in V3A.

We fit the channel response profiles with a Gaussian function and used the FWHM (full width at half maximum) bandwidth of the Gaussian to quantify the neural selectivity. The bandwidths at Post1 (70.08°), and Post2 (74.47°) were significantly smaller than that at Pre (83.74°) (both $t(16) > 4.20$, $p < 0.01$), consistent with the statistical results above.

Effective connectivity analysis of fMRI data

Law and Gold (2009) modeled perceptual learning process as a high-level decision unit refining its connectivities to sensory neurons through response reweighting. Inspired by this, we performed the DCM analysis focusing on the directional connectivities between V3A and IPS and between MT+ and IPS based on BOLD signals from these areas. These three areas were selected for several reasons. First, they are critical brain areas for visual motion processing. Second, the forward modeling analysis has shown that the neural selectivity in V3A for the trained direction increased after training. Third, human IPS, as a putative homologue of monkey LIP (Sereno et al., 2001), has been demonstrated as a pivotal area for motion decision-making (Heekeren et al., 2008; Tosoni et al., 2008; Kayser et al., 2010). Fourth, the modeling work by Law and Gold (2009) attributed motion perceptual learning to the connectivity change between MT and LIP. Bidirectional intrinsic connections were hypothesized to exist between V3A and IPS and between MT+ and IPS. These intrinsic connections could be modulated by the trained and untrained stimuli. Given the extrinsic input to V3A and MT+, we examined feedforward, feedback, and recurrent models for modeling the modulatory effect by the trained and the untrained stimuli (Fig. 7A).

For the trained direction, we computed the exceedance probability of each model (Friston, 2006). The result showed that the feedforward, feedback, and recurrent models had the exceedance probabilities of 64.40%, 28.16%, and 7.44%, respectively, suggesting that the feedforward model was the best one to explain the modulatory effect by the trained direction (Fig. 7B) (note that the recurrent model had more degrees of freedom, so was subject to more stringent criteria). We further compared the modulatory effects at Pre, Post1, and Post2. Relative to Pre, the modulatory effect on the forward connection from V3A to IPS significantly increased at Post1 and Post2 (both $t(16) > 3.09$, $p < 0.05$), but little effect was found with the connection from MT+ to IPS (both $t(16) < 1.38$, $p > 0.05$) (Fig. 7C). For the untrained directions, the exceedance probabilities of the feedforward, feedback, and recurrent models were 88.45%, 11.52%, and 0.03%, respectively, suggesting that the modulatory effect by the untrained directions could also be best explained by the feedforward model (Fig. 7D). However, for the untrained directions, the modulatory effect on the forward connections from V3A to IPS and from MT+ to IPS did not change significantly after training (all $t(16) < 0.98$, $p > 0.05$) (Fig. 7E). These findings suggest that the increased connectivity from V3A to IPS may have contributed significantly to the long-term neural mechanisms of the motion perceptual learning. It is worthwhile to point out that whether or not including MT+ in the model does not affect the connectivity result between V3A and IPS.



Having shown that training increased the forward connectivity from V3A to IPS, it is natural to ask whether training could induce any connectivity change at lower levels in the visual motion processing hierarchy. Accordingly, we built another DCM model containing the connections between V1 and V3A and between V1 and MT+ . We did not find any significant change with the connections after training.

Correlation and regression analyses between psychophysical and fMRI measures

To further evaluate the role of the neural changes revealed in the motion perceptual learning, we calculated the correlation coefficients between the behavioral measure (i.e., improvement in percentage) and the fMRI measures (i.e., the bandwidth change in V3A and the connectivity change from V3A to IPS) across individual subjects. No significant correlation was found between the performance change and the bandwidth change at Post1 and Post2 (Figs. 8A and B). Only at Post1 was the performance change significantly correlated with the connectivity change (Fig. 8C), but not at Post2 (Fig. 8D). These results showed that the performance change could not be well predicted by any of the neural changes alone.

We then built a multiple linear regression model to examine whether the performance change (P) could be predicted jointly by

the bandwidth change (B) and the connectivity change (C) in the following linear equation:

$$P = k_0 + k_b B + k_c C.$$

The interaction between B and C was not included in the regression model to avoid the multicollinearity problem ($B \times C$ and C were significantly correlated). Note also that there was no significant correlation between B and C (Figs. 8E and F). This model provided a good fit for the inter-individual performance change (Post1: $R^2 = 0.51$, $F(2, 16) = 7.2$, $p < 0.01$; Post2: $R^2 = 0.57$, $F(2, 16) = 9.4$, $p < 0.01$). The standardized regression coefficients for B and C were significant at both Post1 and Post2 (Post1: $k_b = 0.50$, $k_c = 0.53$, both $p < 0.05$; Post2: $k_b = 0.67$, $k_c = 0.74$, both $p < 0.01$). These results demonstrated that the performance change could be well predicted by a linear combination of the bandwidth change and the connectivity change.

iscussion

Our study provides the following psychophysical and neuroimaging findings. (1) Motion direction discrimination training improved behavioral performance, which was specific to the trained direction and persisted for at least two weeks. This finding replicated the work by Ball and Sekuler (1987). (2) Immediately after training, the mean BOLD signal in V3A responding to the trained direction decreased,

but this decrease mostly vanished two weeks later. (3) The decoding accuracy and neural selectivity for the trained direction in V3A increased immediately after training and persisted for at least two weeks. (4) The forward connectivity from V3A to IPS also increased immediately after training and persisted for at least two weeks. (5) The behavioral learning effects could be well explained by a linear

combination of the selectivity and connectivity increases. These findings shed light on the long-term neural mechanisms of motion perceptual learning as discussed below.

In this study, we did not use a control group of subjects with “dummy intervention” to demonstrate that the effects we have found are learning specific. Please note, however, that the specificity

investigated here is in regard to specificity of learning with respect to motion directions. That is to say, in the perceptual learning literature, specificity usually refers to specificity of learning to a stimulus attribute, which in our case is motion direction. We considered learning-related changes with the trained direction, after subtracting learning-related changes (if any) with the untrained directions. In this sense, those untrained directions served as controls. In other words, we used within-subjects controls, rather than between-subjects controls.

It has been extensively investigated whether perceptual learning could modulate the mean neural activity in a cortical area. After subjects were trained with a visual detection task, the mean neural activity usually increased (Furmanski et al., 2004; Bao et al., 2010; Hua et al., 2010; Goldhacker et al., 2014), which can be explained by the increased number or improved sensitivity of relevant neural detectors. For studies in which subjects practiced a near-threshold discrimination task, the findings so far are mixed – the mean neural activity was found to increase (Schwartz et al., 2002), decrease (Schiltz et al., 1999; Mukai et al., 2007), or have little change (Op de Beeck et al., 2006; Jehee et al., 2012). We found a mean signal decrease in V3A immediately after the motion direction discrimination training. The interpretation of these learning-related decreases has been that they reflect improved efficiency of processing, manifested as a shift in neural firing from a large population of neurons to a smaller, more specialized subset (Mukai et al., 2007). However, two recent studies on the long-term neural mechanisms of perceptual learning (Yotsumoto et al., 2008; Bi et al., 2014) challenge the view that changes in the mean neural activity are directly related to perceptual learning. Although both studies found an increase in the mean BOLD signal immediately after training, two weeks or one month later, the increase either faded out or did not correlate with the persistent behavioral learning effect. Consistent with these two studies, the absence of the BOLD signal decrease two weeks after training in our study suggests that changes in the mean neural activity to trained stimuli might not be the critical mechanism of perceptual learning.

In contrast to the transient decrease of the mean neural activity in V3A, V3A exhibited a persistent increase in decoding accuracy, suggesting that the long-term neural mechanism of perceptual learning is to make the neural representation of trained stimuli more stable and precise, even in the absence of a change in the mean neural activity. This idea is consistent with other perceptual learning studies on form discrimination (Zhang et al., 2010a), orientation discrimination (Jehee et al., 2012), and motion detection (Shibata et al., 2012). However, it should be noted that these studies only measured the neural changes immediately after training, but not longer-term changes. A more recent study by Bi et al. (2014) identified the long-term neural mechanisms of face discrimination learning as the stability improvement of spatial activity pattern (i.e., higher correlation across multiple measures after training) in left fusiform cortex. This stability improvement finding is in line with our finding here. The improved decoding accuracy in V3A may reflect the sharpening of direction-tuned responses at the population level, as suggested by neurophysiological and modeling works (Schoups et al., 2001; Bejjanki et al., 2011). This is exactly what we found with the forward modeling analysis.

We demonstrated that motion direction discrimination training could refine the neural representation of the trained direction in V3A, but not in MT+. Shibata et al. (2012) also found that motion detection training only affected V3A. These findings seem to contradict the long-standing belief that MT+ is the neural substrate of motion perceptual learning as demonstrated by earlier studies (Zohary et al., 1994; Vaina et al., 1998). Note that, in the earlier studies, human or monkey subjects were trained with only hundreds of trials (as compared to 9600 trials in our study) and the learning effects were short-term. There have been studies suggesting that neural changes in MT are not necessary for motion perceptual learning. Law and Gold (2008) found that motion perceptual learning did not induce changes

in motion-driven responses of neurons in monkey MT (see also Thompson et al., 2013). In a psychophysical study, Lu et al. (2004) found that motion direction discrimination learning was possible with the ‘paired-dots’ motion stimulus that was designed to suppress MT activity (Qian and Andersen, 1994). Although the importance of V3A in motion processing has been well recognized (Tootell et al., 1997; Orban et al., 2003; Bartels et al., 2008; Wall and Smith, 2008), the functional difference between V3A and MT+ is still not clear. Vaina and colleagues (Vaina et al., 2003; Vaina et al., 2005) provided neuropsychological evidence that V3A and MT+ are dominant in local and global motion processing, respectively. In our study, since all dots in the stimuli moved in one direction (100% coherence), subjects’ behavioral learning effect relied on the improvement of their local motion processing ability, which might be reflected as the decoding accuracy improvement in V3A. This hypothesis can be further tested in future research. For example, when subjects are trained with the same task as here, but using noisy motion stimuli, they need to integrate local motion directions to acquire the global direction. In such a case, would MT+ be affected by training?

In addition to the refined neural representation of the trained direction at the sensory area V3A, we also found that VPL could enhance the forward connection from V3A to IPS. To the best of our knowledge, this finding provided the first empirical evidence for the VPL reweighting models (Poggio et al., 1992; Doshier and Lu, 1998; Bejjanki et al., 2011). The reweighting models hypothesize that visual training improves perceptual sensitivity by selectively strengthening the connections from the most sensitive neurons in sensory area(s) to decision units. Although the models are theoretically appealing, they have never been empirically evaluated with connectivity analyses. In our study, V3A became more sensitive to the trained direction after learning. To form an optimal decision or to better read out sensory information, the decision units in IPS need to increase the pooling weight for the output of V3A neurons selective for the trained direction. The weight increase might be reflected as an increase in the forward connectivity from V3A to IPS specific to the trained direction.

It is notable that the representation of the trained direction in IPS, as quantified by the LMIs, did not change after training, which seems to contradict the finding by Law and Gold (2008). Though many differences in stimuli, experimental procedures, and subject species may explain the discrepancy, our view is that, if IPS is simply a decision-making area, its representation of motion direction does not have to be changed by perceptual learning. As suggested by the reweighting models, IPS just gives different weights to different motion channels for making a better decision after training. It seems unnecessary for training to modify the decision-making process implemented in IPS *per se*.

In the DCM analysis, we also measured the effective connectivity between MT+ and IPS, but failed to find any change after training. This finding demonstrated that the increased forward connectivity was not a general phenomenon taking place between low- and high-level cortical areas. It suggests that the connectivity increase is specific to the functional pathway starting from a cortical area (e.g., V3A) that could provide a better representation of the trained stimulus after learning. In MT+, we did not find that motion direction discrimination training altered the neural representation of the trained direction. According to the reweighting model theories, it is not necessary to change the pooling weight or the connectivity strength for the outputs from MT+.

Recently, Beste et al. (2011) discovered a new kind of exposure-based visual learning. They adapted a LTP (long-term potentiation)-like protocol to visual stimulation to alter human visual behavior. Subjects were exposed to passive visual high-frequency stimulation, which induced a long-lasting sensitivity improvement with the exposed stimulus. This finding, as well as other kinds of exposure-based learning (Beste and Dinse, 2013), demonstrated that, unlike our findings here, intensive training may not be necessary for skill learning. However, researchers still know little about the underlying mechanisms of

exposure-based learning. It is worthwhile to explore them for fully understanding the brain plasticity.

Taken together, our results suggest that the neural plasticity mediating perceptual learning occurs not only at the sensory processing stage, but also at the stage of perceptual readout by decision networks. These results help to reconcile discrepancies in the earlier literature on VPL.

Acknowledgments

We thank Zhong-lin Lu for his helpful discussion. This work was supported by the National Natural Science Foundation of China (31230029, 31421003, 91132302 and 90820307) and the Ministry of Science and Technology of China (2015CB351800 and 2012CB825500). Zili Liu was supported in part by a US NSF grant (BCS 0617628) and a China NSFC grant (31228009).

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